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Ecology and Nesting Behavior of *Bombus atratus* Franklin in Andean Highlands (Hymenoptera: Apidae)

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Abstract.—The neotropical bumble bee *Bombus* (*Fervidobombus*) *atratus* Franklin is widely distributed in South America ranging from tropical and subtropical lowlands to high altitudes in the Andes. Most of its biology is known from studies conducted in Brazilian lowland forests and almost nothing is known from other areas, especially at high altitudes. Here we provide data on the nest architecture, brood development, worker behavior, seasonal cycle and associated organisms from seven colonies of *B. atratus* observed above 2000 m of altitude in Colombia and Ecuador. Then, we compare them with those data from Brazil. All colonies found were located above the ground, in disturbed areas. Most of the nests either lacked a defined entrance or had a single entrance; a single nest had five entrances, one of them more active than the others. Nests had from 1 to 8 active queens and up to 80 workers indicating monogynous and polygynous cycles as reported from the lowlands. Nests initially lacked an involucrum covering the brood but eventually developed an irregular involucrum of wax mixed with cardboard and carcasses of *B. atratus* and their associated beetles (*Antherophagus* sp., Cryptophagidae). Bees also built pollen pockets attached to larval clusters for feeding larvae. The average developmental time from egg to adult (29.6 days) and the percentage of cells with two pollen pockets (63.6%) were significantly greater than those previously reported. The maximum pocket diameter was significantly smaller, about half of the size, than those diameters observed in lowland colonies. The ecological significance of such reduction in size is still unclear but could explain the higher frequency of cells with two pockets in our colony. Nests maintained an internal nest temperature about 12°C warmer than external environmental temperature. Several workers were observed constantly scraping and cutting litter on top of one of the nests. Previously this behavior had only been known in *Bombus* (*Fervidobombus*) *transversalis* (Oliver), a closely related Amazonian species. As in the lowlands, *B. atratus* colonies at high altitudes seem to be active year-round. The beetle *Antherophagus* sp. was found in two of the seven colonies observed. They are probably scavengers, but nothing is certainly known about their role within tropical *Bombus* colonies.

Resumen.—El abejorro neotropical *Bombus* (*Fervidobombus*) *atratus* Franklin está ampliamente distribuido en Sur América, encontrándose desde las tierras bajas tropicales y subtropicales hasta las grandes altitudes en los Andes. Gran parte de su biología es conocida de estudios realizados en las tierras bajas brasileras y casi nada se conoce de otras áreas, especialmente a grandes alturas. Aquí proporcionamos datos sobre la arquitectura de los nidos, ciclo de desarrollo, comportamiento de las obreras, ciclo estacional y organismos asociados de siete colonias observadas a más de 2000 m de altura en Colombia y Ecuador. Luego, nuestros datos son comparados con los datos de Brasil. Todas las colonias encontradas estaban sobre el suelo, en áreas perturbadas. La mayoría de los nidos carecían de una entrada definida o presentaban una sola entrada; un solo nido tenía 5 entradas, una de las cuales era más activa que las otras. Los nidos tenían de una a ocho reinas activas y hasta 80 obreras indicando estados monoginicos y poliginicos como ha sido registrado en las tierras bajas. Los nidos carecían de un involucro de cera cubriendo la cría, pero eventualmente desarrollaron un involucro irregular mezclado con cartón y cadáveres de abejas y los escarabajos asociados (*Antherophagus* sp., Cryptophagidae). Las abejas construyeron bolsillos de polen pegados a los grupos de larvas para suministrar el alimento. A diferencia de los registros anteriores, el promedio del tiempo total de desarrollo desde huevo a adulto (29.6 días) y el porcentaje de celdas con dos bolsillos de polen (63.6%) fueron significativamente más grandes. Sin embargo, el diámetro máximo del bolsillo de polen fue significativamente más pequeño, cerca de la mitad del tamaño, que los diámetros registrados en colonias de tierras bajas. El significado ecológico de esta reducción en tamaño es desconocido, aunque podría explicar la alta frecuencia de celdas con dos bolsillos en nuestra colonia. Los nidos mantuvieron una temperatura interna aproximadamente de 12°C mayor que la temperatura ambiental externa. Varias obreras fueron observadas constantemente raspando y cortando hojarasca en el techo de uno de los nidos; este comportamiento habia sido previamente conocido en *Bombus* (*Fervidobombus*) *transversalis* (Oliver), una especie amazónica cercanamente relacionada. Como en las tierras bajas, colonias de *B. atratus* en las grandes alturas son aparentemente activas durante todo el año. El escarabajo *Antherophagus* sp. se encontró en dos de las siete colonias observadas. Probablemente es un reciclador de materia en descomposición, pero nada es conocido con certeza sobre su papel dentro de colonias tropicales de *Bombus*.

Bumble bees (genus *Bombus*) are a diverse group of bees containing 240–250 species worldwide (Williams 1998). They are particularly diverse in temperate areas, although relatively few species are abundant in high tropical environments (Michener 2000). The neotropical bumble bee *Bombus* (*Fervidobombus*) *atratus* Franklin is widely distributed in South America ranging from warm, lowland tropical and subtropical areas to cold, high altitude ecosystems (e.g., Páramo) in the Andes up to 3400 m (Liévano et al. 1991; Chavarría 1996). Such broad geographical and altitudinal distribution suggests the ability to adapt to different pollen sources and environmental conditions. Most of what is known of its biology comes from observations made in lowland subtropical regions of Brazil (e.g., Dias 1960; Sakagami et al. 1967; Zucchi 1973; Cameron and Jost 1998), but reports from other areas, especially high altitudes, are lacking. The principal purpose of this paper is to provide data on the nest architecture, brood development and seasonality of *B. atratus* at higher elevations in the Andes of Colombia and Ecuador.

MATERIALS AND METHODS

A total of seven nests of *B. atratus* were found at two locations as follow: five nests (nests 1–5) from Facatativá (Departamento de Cundinamarca), Colombia, and two nests (nests 6 and 7) from the Botanical Garden "Reinaldo Espinosa" in Loja, Ecuador. Nests were observed from April 1996 to July 1997 (Colombia) and from February 1–19, 2001 (Ecuador). Facatativá is located at 4° 48′ 56″ N, 74° 21′ 54″ W, at 2586 m of altitude. The rainy season is bimodal with maximum rainfall in March–May and another in November (Fig. 1). The mean monthly precipitation is 689 mm and the median annual temperature is 12.4 °C (IGAC 1996). Loja is located at 2152 m and has a mean monthly precipitation of 900 mm, with most precipitation falling between December–March. The median annual temperature is 15 °C.

All Colombian nests were carefully opened and their contents recorded. Only nest 1 was captured and transferred to the Laboratorio de Investigaciones en Abejas (LABUN) of the Universidad Nacional de Colombia in Bogotá (Colombia) for closer examination. The nesting site volume was

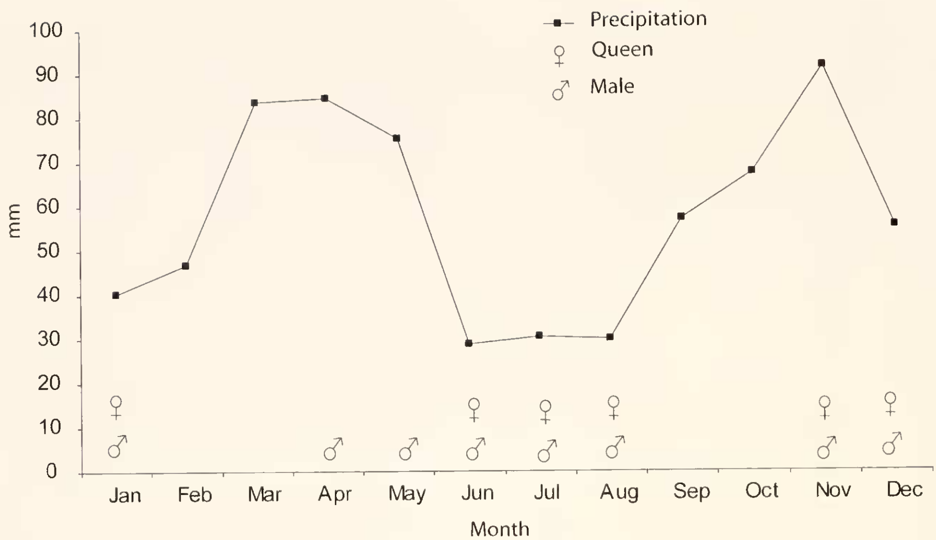

Fig. 1. Seasonal collections of queens and males of *B. atratus* in Facatativá (Colombia). Workers were found in every month.

considered as the space occupied by the brood. We multiplied the maximum and minimum diameters in cross section by the maximum height of the brood to approximate this volume. The angle of the slope of the nesting area was estimated with a compass. Observations on brood development were taken *in situ* every other day only from nest 2 over 35 days by mapping brood cells from the time of their construction to adult emergence. Cells containing larvae were easy to recognize by the presence of pollen pockets (Michener 1974), their circular shape and dark brown color derived from the pollen/wax mixture from which they are constructed. Cells containing pupae are oval-shaped and yellowish as the pollen/wax exterior is scraped off to expose the silken cocoon. The duration of the egg stage was estimated based on the construction of pollen pockets, which were generally built a day after the larva hatched. To determine the seasonal cycle of *B. atratus* in Facatativá, the insect collections of LABUN and Instituto de Ciencias Naturales of the Universidad Nacional de Colombia (Bogotá, Colombia) were examined. Only those specimens collected between 2550 m and 3200 m of altitude from Facatativá and contiguous areas (less than 50 km^2) (e.g. Madrid, Mosquera), were included and the caste recorded. About 200 specimens were examined.

Internal nest temperature and external ambient temperature taken in shade were recorded using a digital thermometer (Reotemp® Digital TM99-A) placed directly inside the nest through one of the sides. Temperature readings started once colony disturbance died down, from 10:00 to 18:00 hrs, at intervals of 1 hr. Measurements were made only on nest 2 on January 24–26, February 1, 7–8, 1998. All measurements are given with standard errors. A t-test was used to assess significant differences between the diameter of primary and secondary pollen pockets, and between internal and external nest temperatures. All statistical analyses were performed on a personal computer using MINITAB® 14 for windows®.

Voucher specimens of *B. atratus* and associated organisms are deposited in the LABUN collection (G. Nates-Parra) and Museo Nacional de Historia Natural,

Table 1. *Bombus atratus* nests observed in Facatativá, Colombia. A = volume of nesting area (cm³); B = number of egg cells; C = number of larval clusters; D = number of pupae; E = total number of cells; † = number of queens; w = number of workers; m = number of males. (−) = data not recorded.

Nest	Location	A	B	C	D	E	†	w	m	Observation dates
1	Pasture	—	—	—	—	598	8	63	0	Apr 27–May 22 1996
2	Eucalyptus forest	11250	15	20	70	105	1	80	0	Jun 30–Aug 4 1996
3	Eucalyptus forest	7163	4	11	10	25	2	7	3	Jan 31–Feb 6 1997
4	Pasture	3300	3	2	12	17	8	20	0	Feb 8–29 1997
5	Eucalyptus forest	1300	9	2	26	37	1	8	0	Jul 3–30 1997

Universidad Nacional Mayor de San Marcos, Lima, Perú (G. Lamas). A videotape of the nest site and instances of worker behavior on top of nest 7 in Ecuador is available from CR.

RESULTS

Nest Site and Nest Architecture

All colonies found were located above the ground. Nests in Colombia were constructed within dense bunches of grass (~40 cm height), in open, highly disturbed areas such as grazing pastures for cows and horses with scattered exotic trees such as *Eucalyptus* (Myrtaceae) and *Pinus* (Pinaceae). Nests were situated on flat ground or slopes inclined at angles of 20–30°. Nests 2, 3 and 5 were found inside *Eucalyptus* plantations; the first two were 3 m apart and nest 5 was about 420 m away from the others. Nests 1 and 4 were in a contiguous pasture area about 80 m from nest 5. Both nests 6 and 7 from Loja were found in shaded areas of the botanical garden, among *Pinus* trees, with their entrances facing west. Bees used grass as the main construction nest material mixed with dry *Eucalyputus* leaves or, in the case of nests 6 and 7, needles of *Pinus*. Three nests had a single nest entrance (about 2 cm in diameter, n = 2) that consisted of an irregular hole in the roof of the nest. One nest (nest 7) had five entrances, one of them more active than others and subject to modification in shape by workers over time. The remaining nests did not have a well-defined nest entrance. All nests lacked a waxen envelope (involucrum) covering the brood. However, during the first days of observations on nest 2, it developed a weak waxen involucrum mixed with small pieces of cardboard and carcasses of *B. atratus* and beetles (*Antherophagus* sp., Cryptophagidae), that eventually covered almost the entire brood. Nests approximated a circular shape with a diameter that ranged from 10–30 cm (X = 20 cm, ± 1.7, n = 12), height from 10–18 cm (X = 13.3 cm, ± 1.3, n = 6), and an average volume of 5753 cm³ (Table 1).

Brood Development

The brood comb in all examined nests was located in a slight depression in the ground (4–5 cm deep) and, as previously recorded for *B. atratus* and various other bumble bee species, active brood cells were built on top of old, decayed cocoons, thus resulting in an upward expansion of the brood (Sakagami et al. 1967; Taylor and Cameron 2003). Egg cells were on average 5.2 mm in diameter (± 0.1, n = 26) and contained from 4 to 15 eggs (X = 9.4 ± 1.1, n = 8). Individual eggs were 3.8–4 mm in length and were piled horizontally, one over the other, or sometimes were vertical at right angles to the cell axis. The egg cells were built at a rate of 1.5 cells per day. Twenty-six of 50 (52%) cells observed from first stages of construction did not reach adult emergence; 19 were destroyed by workers at the egg cell stage and 7 at the pupa stage, after the brood died. The cause of death is unknown.

Pollen pockets were constructed and attached to larval clusters for feeding larvae,

Table 2. Comparative aspects of the nesting biology of *B. atratus* from lowlands [data from Sakagami *et al.* (1967)] and high altitudes (This study). * = data from Laverty and Plowright (1985). § = duration in days, range is given in parenthesis followed by its standard error.

Biological Aspect	Lowland	Highlands
§ Duration eggs	6	6.8 (5–11) ± 0.4, n = 25
§ Larval stage	12–13	10.9 (8–14) ± 0.3, n = 21
§ Pupa	8–12	12.8 (10–15) ± 0.3, n = 15
§ Total time egg-adult	*26.7 (24–34) ± 0.8, n = 7	29.6 (28–31) ± 0.3, n = 15
Pollen pockets/cell	1–3	1 and 2
Freq. one pocket	74 %	36.4 %
Freq. two pockets	21 %	63.6 %
Freq. three pockets	5.3 %	0
Pocket diameter (mm)	7.3 (4–10) ± 0.1, n = 177	3.7 (3-6) ± 0.1, n = 80

as previously noted in *B. atratus* and other species of the subgenus *Fervidobombus* (Sakagami et al. 1967; Sakagami 1976; Taylor and Cameron 2003). These pockets were usually made one day after the larvae hatched, generally between the sixth and seventh day after the queen laid the eggs, and remained for a period of 6.5 days on average (n = 22 cells). Eight and 10 larval cells had one and two pockets, respectively, throughout the feeding period; however, bees built a second pocket for four of the eight cells several days after the first one was built and in one case, bees destroyed one of the two pockets initially built. The maximum diameter of the secondary pockets ranged from 3 to 6 mm (X = 3.7 ± 0.1, n = 80) and there was no statistical difference in the mean diameter between the two pockets (*t-value* = 0.53, $P > 0.01$).

The total developmental time from egg to adult observed in our study is within the range found by Sakagami et al. (1967) and Laverty and Plowright (1985) for lowland *B. atratus* colonies (Table 2). However, the average value for the developmental time was significantly longer in our study than that reported by Laverty and Plowright (1985) (*t-value* = 4.53, $P < 0.01$).

Nest Thermoregulation

Internal nest temperatures ranged from 23.8–29.9 °C (X = 27.2 °C ± 0.3, n = 35) and remained about 11.5 °C warmer than external ambient temperatures (X = 15.7 °C ± 0.9, range = 5–22.5 °C, n = 26). Internal nest temperature was significantly higher than external ambient temperature ($P < 0.01$, t-test).

Worker Behavior

An approximate number of nine workers from nest 7 were observed manipulating litter persistently on top of the nest. These workers actively walked around, constantly scraping litter with their mandibles and pushing the litter beneath their body with the help of the forelegs, as reported for *Bombus* (*Fervidobombus*) *transversalis* (Oliver) (Cameron et al. 1999). Small pieces of litter were simply moved out of the way whereas larger pieces, such as large leaves mainly found at the margins of the nest area, were cut into small pieces (≪2 cm). During the observation period, bees were not seen bringing pieces of litter in or out of the nest. The specificity of these workers to work on top on the nest could not be established since they were not individually marked. This behavior was not noted on the nearby nest 6 in Ecuador or on any of the Colombian nests.

Colony Life Cycle and Seasonality

The number of queens and workers per colony in the Colombian nests at the times they were found ranged from 1–8 queens and from 8–80 workers. Males were only present in a single small colony (Table 1). The colony size of the Ecuadorian nests could not be established; however, a total of four dead queens in different degrees of decomposition were found outside the entrance of nest 7 upon discovery. One of the queens was partially buried in the ground. Later on February 19, at the same nest, other two dead queens and three workers were found outside the nest entrance; one of the two queens lacked wings. Males were collected foraging on flowers around the nesting area in Ecuador.

Appraisal of museum specimens revealed that workers of *B. atratus* had been collected in every month of the year from Facatativá and surrounding areas, whereas queens and males were collected only during periods of the year with less precipitation (Fig. 1).

Associated Organisms

Beetles of the genus *Antherophagus* were found inside the old comb and debris of the nest, at the bottom of the comb in two of the five observed colonies from Facatativá. They were more active and frequently seen in upper areas of the nest where they tried to reach foragers during the terminal phase of the colony. They were also regularly seen attached to the hind legs of workers at flowers.

DISCUSSION

All nests were found on the ground and covered with vegetable material as previously reported for *B. atratus* at lower altitudes. None of the dissected nests (nests 1–5) had a waxen involucrum covering the brood when found; however, as reported by Sakagami et al. (1967), this species can eventually develop a thin layer of waxen involucrum mixed with dead leaves and dead insect parts. The use of man-made materials to build the involucrum such as cardboard is reported for the first time. The origin of the cardboard is unknown and no bees were observed bringing or collecting such material; nonetheless, it is likely that the cardboard was present at the nest site prior to the establishment of the colony since most bumble bees modify the materials available at the site of nest construction (Michener 1974). The construction of the involucrum by nest 2 was likely a response to mechanical disturbance when taking observations of the nest, but may also be a strategy to protect the nest during inclement weather. Further observations are required to determine this.

The observation of workers manipulating and cutting pieces of litter on top of the nest in Ecuador is very similar to behavior otherwise known only in the Amazonian bumble bee *Bombus transversalis* (Cameron et al. 1999), but it is not surprising in a phylogenetic sense. In fact, molecular and morphological analyses suggest that *B. atratus* comprises a clade with *B. transversalis* and *B.* (*Fervidobombus*) *pullatus* Franklin (Cameron and Williams 2003). The latter two species are the only primarily tropical rain forest species of *Fervidobombus*. The fact that leaf-cutting behavior was seen only at one of the Ecuadorian nests, and at none of the Colombian nests, suggests variability in the expression of this behavior. More observations are necessary to determine the ontogenetic or seasonal, if any, components that may influence leaf-cutting.

Bombus atratus is perhaps the only neotropical bumble bee that exhibits a broad plasticity in nest site selection, ranging from cavities constructed below ground (Cameron and Jost 1998) to aerial nests built in trees (Dias 1960). It is found in forest, savanna, and highly disturbed grassland, as reported in this note. This flexibility in nesting habit, as well as the ability to use exotic pollen sources (Liévano and Ospina 1984; Gonzalez unpublished data), are likely important factors enabling this species to inhabit diverse environments.

Bombus colonies from temperate areas have a typical annual cycle and one queen per colony. Tropical lowland colonies of *B. atratus* are considered perennial, switching between polygynous and monogynous cycles (e.g., Moure and Sakagami 1962; Zucchi 1973; Cameron and Jost 1998). The colonies observed in our study had from one to several queens. Although we have no data, it is possible that more than one of these queens was reproductive inside the nest. The dead queens found outside the entrance of nest 7 hints at the possibility that this nest had recently gone through a polygynous phase that led to the death of all but one queen (Cameron and Jost 1998). Additional observations (R. Ospina pers. comm.) of multi-female nests of *B. atratus* in the Andes corroborate such cycles of polygyny and monogyny. Queens and probably males may be active outside of their nests throughout the year even though specimens of these castes were not seen in collections from Facatativá and vicinity during the rainy periods. Queens and males have been collected during March and September–October in less seasonal areas than Facatativá at similar altitudes (e.g., La Calera; Gonzalez pers. obs.) and therefore are present during every month of the year at these altitudes. Thus it may be possible for *B. atratus* to initiate new colonies at any time of year, as noted for *Bombus* (*Pyrobombus*) *ephippiatus* Say from the highlands of Costa Rica (Laverty and Plowright 1985).

In general, our observations on the brood development of nest 2 agree with those of Sakagami et al. (1967) from a single captive colony. The most striking differences between the studies, however, are in the frequency of the number of pollen pockets per cell, pocket diameter and the total developmental time. Although our sample size was about half the number of cells observed by Sakagami et al. (1967), our nest had, in proportion, more cells with two pollen pockets. The maximum diameter of the pollen pockets observed in our colony was significantly different, about half the diameter of those observed by Sakagami et al. (1967) (*t-value* = 19.53, $P < 0.01$; Table 2). In addition, their colony had cells with three pollen pockets. The ecological significance of such reduction of the pocket size in our colony is unclear but could explain the higher frequency of cells with two pockets. Additional observations on different colonies are needed to understand the significance of the pollen pocket numbers.

The longer average value for the developmental time from egg to adult observed in our study than that reported by Laverty and Plowright (1985) was somewhat expected. Low temperatures at high altitudes might delay development, though, as we show here, *B. atratus* colonies are able to keep their internal nest temperature higher than external ambient temperature; however, they would have to invest more energy to do this at cooler temperatures. Our data support other observations (Laverty and Plowright 1985) that brood development times in neotropical species are on average longer than those for temperate bumble bees.

Although tropical high altitude environments are relatively cooler year-round, they experience large daily changes in weather conditions, which influence diurnal flight activity. Foraging under such conditions may be restricted to taxa such as bumble bees that can effectively regulate body temperature (Heinrich 1979; Bishop and Armbruster 1999). Our data show that, as in other bumble bee species (e.g., *B. transversalis*, Taylor and Cameron 2003), workers in *B. atratus* nests can maintain a stable nest temperature warmer than ambient, presumably by incubating the brood cells through heat produced by muscular contractions (Heinrich 1979). Regulation of body and nest temperature can be particularly important and even critical for bees at high altitudes where air temperature can quickly change from several degrees below zero up to 23 °C. For instance, small sleeping aggregations of males of solitary Andean bees such as

Thygater aethiops Smith (Apidae, Eucerini) are occasionally found dead, frozen and hanging on leaves when temperatures reach several degrees Celsius below zero (Gonzalez and Engel in press). Thus, if the maintenance of internal nest temperature in *B. atratus* depends on colony size, larger colonies are likely to be favored over smaller colonies in such Andean environments. Nonetheless, our colonies were smaller than those reported in lowland environments.

The association between *Antherophagus* beetles and *B. atratus* was first noted by Roubik and Wheeler (1982) from a colony kept in captivity in Bogotá, Colombia at 2600 m of altitude. Species of *Antherophagus* have also been reported from neotropical bumble bees such as *B. ephippiatus* from Costa Rica (Chavarría 1994). They are probably scavengers, given that they are found within the nest debris in healthy colonies, but besides these reports nothing is known about their role within tropical *Bombus* colonies.

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